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Differentiation of the bite force response was investigated by training rats to obtain water reinforcement by emitting bites with peak forces within 4 different 500-gm.-wide bands of forces. All subjects learned to bite with peak forces within each of the required bands, although the average maximum percentage of correct bites per session was only approximately 70%. Data were compared with those from studies of differentiation of the paw-press force response, and it was concluded that the differentiation process is similar in the 2 dissimilar response systems. Because of the generality of differentiation findings across motor systems, it was suggested that methods and results from studies of response differentiation might be used to increase our understanding of motor system function.

Response differentiation has been investigated by Skinner (1938), Herrick (1964), Notterman and Mintz (1965), Ferraro, Grilly, and Tang (1968), and Filion, Fowler, and Notterman (1970). The results of these studies suggest that a response should not be considered as a "go-no-go" situation, but rather as one in which quantitative components or subcategories of the response, such as force or duration, must be taken into account. These components are present in every response, and in every learned action some type of differentiation of response components takes place. For example, the ubiquitous microswitch behind levers and keys in the usual operant bar-press or key-peck apparatus determines the force and duration of movement which must be emitted by the subject in order that the movement be accepted as a valid response. The subject gradually learns, through the process of response differentiation, the particular force and/or duration which must be applied in the case of each individual operandum. The process of response differentiation is essentially the same as that of stimulus discrimination, with the exception that differentiation is based on internal response-produced stimuli, while discrimination is based on exteroceptive stimuli.

Although response differentiation may be of theoretical interest to behaviorists, it is potentially more important from an applied standpoint to those involved in the study of the functioning motor system. The methods used in and the results obtained from studies of response differentiation can be used to view in detail the behavioral processes involved in the acquisition of motor responses. Combining this knowledge of behavioral processes with that of neural processes obtained from neurophysiological studies of the motor system, it may be possible to increase our understanding of the way in which the motor system uses feedforward and feedback mechanisms, preprogrammed neural subroutines, and various types of sensory input in motor learning and performance.

However, in order for the tool of response differentiation to be of use in the study of motor systems, it is necessary to show that the behavioral results obtained in studies of differentiation, such as those mentioned previously, are applicable to a number of different motor responses. Previous research in this area has dealt only with the paw-press response. Although consistent results have been obtained from this response system, it is possible that these results reflect only factors specific to this particular system, rather than factors common to all

[1] This paper is based on portions of a dissertation submitted to the Department of Psychology, Stanford University, in partial fulfillment of the requirements for the PhD degree.

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motor response systems. The present research, therefore, investigated another response system, the bite response system, in order to determine the generality of previous findings with respect to other motor response systems.

The bite response system was chosen for a number of reasons, in addition to its dissimilarity to the paw-press system. These reasons are as follows: (*a*) The bite response has no possible visual feedback, and thus no steps need be taken to eliminate this exteroceptive cue when one wishes to study motor learning based solely on response-produced feedback; (*b*) the bite response is very natural to most subjects, especially when it results in the direct acquisition of food and water; (*c*) from an evolutionary standpoint, food gathering and consumption are the most primitive of organized functions of living organisms, thus suggesting that control systems for these functions are well organized, but somewhat less complex, than those for more recently evolved functions.

The current research deals primarily with the differentiation of response force. Notterman and Mintz (1965) have described in detail the differentiation of paw-press force in rats. Of special interest to the present study are their data on differentiation under band criteria. In studies of differentiation under band criteria, reinforcement is made contingent on bar presses with peak forces lying between a lower and an upper limit of force. Among the important findings obtained from this investigation were that (*a*) rats learned to press a bar with peak forces appropriate to the force criteria upon which reinforcement was contingent; (*b*) on the average, the maximum level of performance or percentage of correct responses was around 55%–65%; and (*c*) there was a high positive correlation between force of response and duration of response. In the present study the methodology used by Notterman and Mintz was followed as closely as possible, so that bite force differentiation could be compared with that of paw-press force. From this comparison some conclusions can be drawn concerning the generality of response differentiation within different motor response systems.

Method

Subjects

Nine male Long-Evans rats weighing 400–500 gm. and 7–20 mo. old served as subjects. Each animal was individually housed in an animal holding colony and was kept on a water-deprivation schedule during the course of the experiment to maintain body weight at 80% of ad-lib body weight. Standard laboratory rat chow was available on an ad-lib schedule.

Apparatus

The essential components of the system used to measure bite force and duration, to determine whether these components of the response met various preset requirements, and to deliver water reinforcement, consisted of a strain-gauge force transducer attached to a titanium bite piece, and an IBM 1800 data acquisition and control system. The grooved bite piece was triangular in shape (when seen in cross section) with the base 1.5 cm. wide and 2.0 cm. long. The grooves, located near the apex of the triangle, ensured that the animal would always bite in the same place, and thus that the force reading would be accurate and reliable. In addition, the grooves caused the bite to be essentially isometric, the distance between the subject's upper and lower incisors during biting being approximately .5 cm. The strain gauge was calibrated for forces within the 0–2,700 gm. range, with 1 gm. yielding 1 mv. The response of the device was shown to be linear within this range, and accuracy was estimated to be within 10 gm. In the center of the bite piece was a piece of 18-ga. stainless steel tubing through which water from a gravity feed system could be presented directly into the subject's mouth.

The analog signal from the force transducer was sent directly into the IBM 1800 computer. The computer sampled and digitized input signals above 400 mv. at a 1 msec. per point rate. Requirements for the maximum bite force and for the minimum bite duration were set into the control program at the beginning of each session. If (*a*) the maximum force of the bite was within the preset required band of forces and (*b*) the duration was greater than the preset, required minimum duration, then at the end of the bite, when the force dropped below the 400-gm. level, the computer effected a contact closure which resulted in the subject's receiving .03 cc of water as reinforcement. The maximum or peak bite force, the total bite duration, and the interbite interval were stored in the computer after each bite and were dumped to magnetic tape at the end of each day's group of trials.

The bite transducer and the cradle for the restraining cage were situated in a standard Lehigh Valley rat chamber located inside a room specially shielded from electrical and acoustical noise. Subjects were tested in a cylindrical wire-mesh restraining cage (18 cm. long and 8 cm. in diameter), which could be mounted in the cage cradle so that the bite piece protruded 3 cm. into the front of the restraining cage at the level of the rat's mouth. The onset of cue lights, located 7.5 cm. behind the bite piece and 3.5 cm. to either side and above it, and a tone signaled times during which reinforcement would be available should the subject make the correct response.

Procedure

Pretraining. Using water as the reinforcer, subjects were first trained to bite with peak forces greater than 400 gm. This phase of pretraining was usually accomplished within 3 ½-hr. sessions. The 400-gm. level was chosen as the minimum force criterion because bites of lower peak forces tended to run together and to be hard to distinguish as discrete bites. Bites with peak forces under this criterion level were not read by the computer and thus were not considered responses. Reinforcement was delivered upon the termination of the bite, i.e., when the force returned below the 400-gm. level. This procedure insured that the bite, as a whole, discrete response, would be reinforced, and it prevented the reinforcement of some particular level of force as it was reached.

Once subjects had attained a constant rate of responding, as determined by an examination of cumulative records, they were given training on a cued 3-sec. differential reinforcement of low rates schedule. This schedule required at least a 3-sec. separation between every response. Availability of reinforcement was signaled by the onset of tone and light cues. When the subjects had learned to respond correctly on this schedule, they were placed on a 3-sec. fixed interval schedule. Under this condition, responses with peak forces greater than 400 gm. were reinforced if they occurred at least 3 sec. after the previous correct response. Thus, when tone and light cues were turned on, the animal would bite, then get reinforced if the bite were forceful enough, and the tone and light cues would then go off for 3 sec. During this 3-sec. blackout, no bites would be read by the computer. At the end of the blackout, the cues were again turned on and reinforcement was available for a correct response. When subjects learned to respond primarily during the times when the cues were on, they were moved to the training phase of the experiment. Pretraining usually took 10–14 daily sessions.

Training. In this phase of the experiment, subjects were required to bite with peak forces within certain ranges or bands of forces when the cues were on. If the peak force of a bite was below a lower limit or higher than an upper limit of forces, no reinforcement was given. Five different bands were used: Band A = 700–1,100 gm., Band C = 1,100–1,500 gm., Band D = 1,500–1,900 gm., Band E = 1,900–2,300 gm., and Band F = 2,300–2,700 gm.

Eight animals received training on an ascending series of Bands A through E. These subjects were given 16 daily trials at each band level. Each trial consisted of 100 bites and lasted 6–10 min., depending on the response rate of the particular subject. On Band A, for example, subjects were reinforced when they emitted bites with peak forces greater than 700 gm. but less than 1,100 gm. when the cues were on. Reinforcement was presented for bites with peak forces within the required band upon termination of the bite. No bites during the 3-sec. blackout were accepted or reinforced by the computer.

One additional subject received training on an ascending (Bands A through F) and a descending (Bands F through A) series. For this animal, as many daily trials of 100 bites were run as were needed to produce relatively stable performances at each band level. Stability was determined by observing the learning curves and the mean peak force curves.

Results

Learning curves for the ascending training series are shown in Figure 1. These curves show the percentage of responses which were reinforced in each trial averaged over the 8 subjects. It can be seen that these subjects were able to increase the number of reinforced responses obtained per trial over the course of the 16 training trials. By the sixteenth trial, under all but the Band D condition, the subjects were ob-

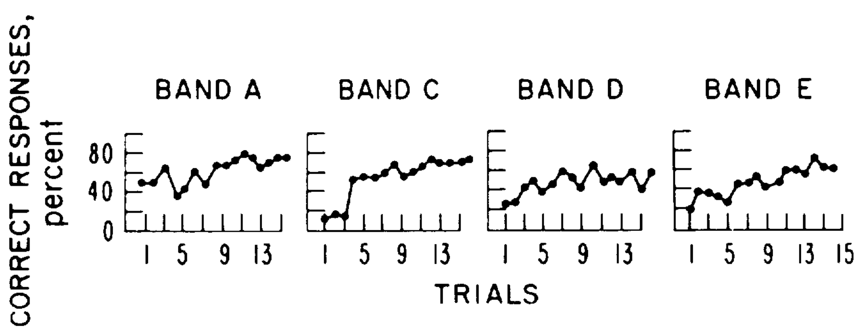

FIG. 1. Learning curves from the ascending training series.

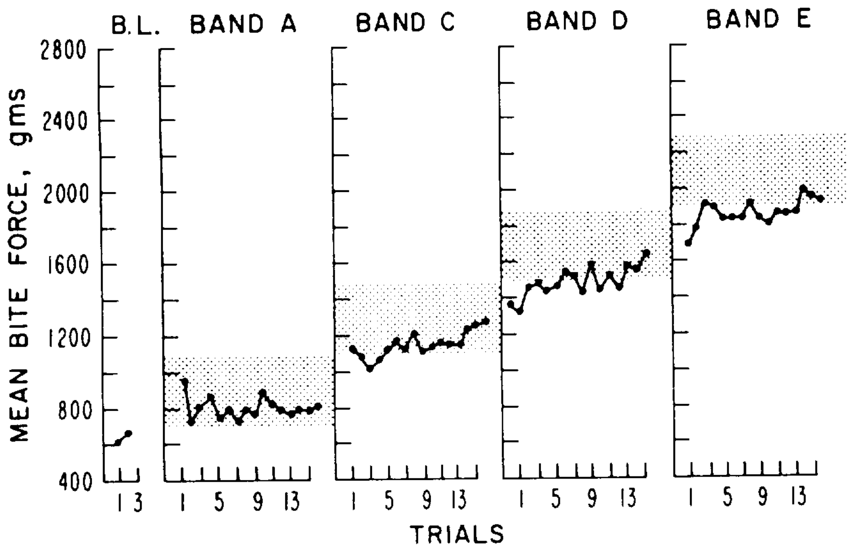

FIG. 2. Mean peak bite force per trial from the ascending training series. (Abbreviation: B.L. = base line [no band requirement].)

taining reinforcement for approximately 70% of their bites. In individual cases, the percentage of correct responses sometimes rose as high as 85%. For certain subjects the learning curves reached an asymptote within the 16 trials. For other subjects, it appears that further learning would have occurred if further trials had been given.

Figure 2 permits the comparison of the mean peak force per trial, averaged over all subjects, with the required force band. This figure strikingly shows that the reinforcement criteria did control the level of the emitted bite forces. Another important factor to note in Figure 2 is the rapidity with which the changes in the force requirements were adjusted to by the subjects. In Band C, for example, it appears that on the average subjects adjusted to the change very quickly, since even during the first trial the mean peak forces emitted were very close to the required force. There are, however, individual differences in the rate at which subjects learn a new criterion. This rate is somewhat dependent upon the band level, with individual subjects adjusting to Bands A and C within the first or second trial, and Bands D and E within the second to the fifth trial.

Figure 3 represents the mean duration of bites within each of the 16 trials for each band averaged over all 8 subjects. It can be

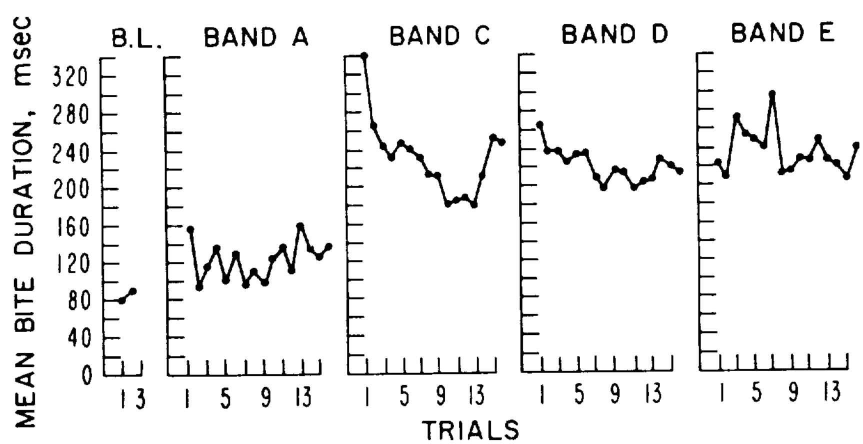

FIG. 3. Mean bite duration per trial from the ascending training series. (Abbreviation: B.L. = base line [no band requirement].)

seen that the mean duration increased along with the increase in mean peak force for continuous reinforcement (pretraining), Band A, and Band C, thus reflecting a positive correlation between peak force and duration. For Bands D and E, however, the averaged mean duration tended to remain relatively constant. Four of the 8 subjects showed high positive correlations between peak force and duration regardless of the band level (mean correlations for last 2 trials in each band were between .50 and .60), while for the other 4 subjects the comparable correlations were much lower, although still positive (between .17 and .34).

Relative variance, i.e., the ratio of the standard deviation to the mean, was found for peak force and duration and was averaged over all 8 subjects (Croxton, 1959). These data show that the relative variance of peak force was much lower (between .1 and .3) than the relative variance of duration (between .3 and .7). The relative variance of peak force decreased slightly (approximately .10) over the course of the 16 trials within each band, but showed almost no decrease (approximately .05) across bands. On the other hand, relative variance of duration decreased greatly both within (approximately .25) and across (approximately .40) Bands A through D, but apparently stabilized under Band E. For individual subjects the average relative variance of peak force ranged from .06 to .57, while the average relative variance of duration ranged from .22 to .99.

One subject was trained on both an ascending and descending series of bands in order to test whether the results obtained using the ascending series might be due to order effects inherent in that series, rather than to any true differentiation. This subject generally attained an asymptotic level of performance, in which at least 70% of the responses were correct in both the ascending and descending series. The force criteria controlled the mean peak force per trial in the same way for the descending as for the ascending series. The relative variance of peak force for each trial decreased from Band A to Band E in the ascending series and remained quite low (around .12) for the remainder of training, regardless of the band criteria. This result suggests that the relative variance of force is not a function of any particular band or level of learning, but rather a function of the amount of experience with the bite task.

Discussion

From the data presented in the previous section it is possible to conclude that rats can learn to differentiate their bite force in much the same way as they learn to differentiate their paw-press force. That the increase in force seen in the ascending band series is not attributable to order effects is evidenced by the fact that the same control of bite force by the reinforcement criteria is shown for the subject tested in the descending series.

Animals in the bite force experiment actually appear to have attained higher levels of differentiation, i.e., a greater percentage of correct responses, than did those in the paw-press experiments of Notterman and Mintz (1965). The fact that the subjects in the present experiment learned to emit more correct responses might be due to a difference in procedure. As was noted previously, the present experiment requires the subject to wait a minimum of 3 sec. between bites. No such restriction was placed on animals in the paw-press experiments. This restriction prevents subjects from responding so fast that it is impossible for the reinforcement to be linked to a bite which actually was correct and merited the reinforcement. Without this restriction it might well be difficult for the subject to discriminate exactly which component of the response is being reinforced. A comparison of learning curves for bite force obtained with and without the 3-sec. blackout restriction, collected from an earlier pilot study, indicates that the best performance (in terms of the percentage of correct responses after 10–15 trials) is approximately 10% higher in the case in which the 3-sec. blackout was used. Were the same 10% increase to be found if the blackout procedure were used in Notterman's experiments, the results of the paw-press and the bite force differentiation research would be almost identical as far as level of performance or learning is concerned.

Notterman's results, showing a high positive correlation between peak force and duration, were obtained for 5 out of 9 of the animals in the present study. This high correlation makes it difficult to know which component of the response, peak force or duration, is actually controlled by the reinforcement. The present research suggests that the relative variances of the 2 components might give a clue to the solution of this problem. As noted previously, when force criteria are in effect and the force of the response is being reinforced, relative variance of peak force is much lower than that of duration. On the other hand, preliminary data from a study dealing with the differentiation of response duration indicate that when duration criteria are in effect and the subject is being reinforced for specific durations, the relative variance of duration is as low as or lower than that of peak force.

In both Notterman's and the present study, an asymptote in the learning curves was obtained that was well below the perfect performance level. Notterman and Mintz (1965) explain their maximum level of performance by invoking a hypothesis involving a self-imposed schedule of reinforcement. However, there appears to be little need to use such an unparsimonious explanation as self-imposed scheduling to explain a less-than-perfect level of performance. Other more objective explanations are available. For example, a blackout procedure, such as that used in the present study, which presumably clarifies the conditions of reinforcement for the subject results in a higher level of performance. Procedural, motivational, and physiological factors should first be examined as determinants of level of performance in tasks involving differentiation of force under band criteria before resorting to more complex and less readily testable factors.

One can conclude from this study that the differentiation of the bite force response is based on neural mechanisms and behavioral processes similar to those mediating the paw-press response, and that previous findings based on the paw-press response can be accepted as reflecting motor system mechanisms common to other response systems. It is necessary to determine what these mechanisms are, however, before the methods employed in and the results obtained from studies of response differentiation can be used to further our understanding of the functioning motor system in the intact, behaving organism.

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